

# *Lysinoe* (Gastropoda: Pulmonata) and Other Land Snails from Eocene-Oligocene of Trans-Pecos Texas, and Their Paleoclimatic Significance

by

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**Abstract.** A large helminthoglyptid land snail, *Lysinoe breedlovei* spec. nov., occurs in the Colmena Tuff and Chambers Tuff of the Vieja Group, Presidio County, Texas, associated with vertebrates of the Candelaria and Porvenir local faunas respectively. *Lysinoe breedlovei* is also present in correlative strata in the Agua Fria-Buck Hill area of Brewster County, Texas, and in a predominantly marine sequence in Nuevo León, Mexico, associated with a "Vicksburg" molluscan fauna. Associated vertebrate assemblages from the Texan localities have been assigned to the Uintan and Chadronian North American Land Mammal "Ages." Radioisotopic dates indicate a time span of about 41-38 Ma before present. The species is strikingly similar to the Holocene *Lysinoe ghiesbreghtii* (Nyst) from southern Mexico and Central America. Climatic and ecological parameters from the range of *L. ghiesbreghtii* imply that conditions in this part of Texas during the late Eocene-early Oligocene were moist and temperate and that the prevailing vegetation was probably an ecological analogue of the seasonal temperate forests of present-day Chiapas, Mexico. Mean annual rainfall in excess of 123 cm, either with or without a winter dry season, is indicated. Many plant species of the temperate Mexican forests have similar or identical counterparts in the southeastern United States. *Lysinoe* supports the concept of a formerly continuous forest distribution around the northwestern Gulf of Mexico.

The Candelaria local fauna also includes the helminthoglyptid genus *Polymita*, now confined to Oriente Province, Cuba. Other land snails from the Chambers Tuff include two subgenera of *Pleurodonte* (Camaenidae), now confined to Jamaica and the Lesser Antilles, and *Xerarionta* (Helminthoglyptidae), now living from southern California to southern Baja California. *Polymita* and *Pleurodonte* both now inhabit more tropical forests than *Lysinoe*. *Xerarionta* inhabits arid and semiarid zones within the influence of Pacific fog. By analogy with plant communities, climatic equability may have permitted the co-occurrence of genera that now show conflicting climatic preferences. The snail assemblages document a general southward retreat of land mollusk genera through the Tertiary and a developing allopatry.

## INTRODUCTION

THE VIEJA GROUP of Trans-Pecos Texas and adjacent Chihuahua, Mexico, consists of about 800 m of interbedded sedimentary, volcanic, and volcanoclastic rocks of Eocene and Oligocene age. The vertebrate fossils are well studied, particularly in the so-called Rim Rock Country lying between the Rio Grande and the Sierra Vieja of Presidio and Jeff Davis counties. This area is paleontologically important because a number of radiometric dates have been obtained, in either association or superposition

with described vertebrate faunas (EVERNDEN *et al.*, 1964; WILSON *et al.*, 1968; WILSON, 1971, 1978). WILSON *et al.* (1968) mentioned in passing the presence of gastropods in rocks of the Vieja Group. PAMPE (1974) described and illustrated Vieja Group gastropods in his brief report, applying existing names from the literature of the Rocky Mountain and Great Plains regions. He evidently believed them all to be fresh-water forms; my identifications differ entirely from his. WILSON (1978) included gastropods (mostly unidentified) in his comprehensive Vieja Group faunal lists.

The Rim Rock Country is part of an unstable zone along the western flank of the late Paleozoic Diablo Platform which coincides with the eastern edge of the Mesozoic Chihuahua Trough. During late Cretaceous/early Tertiary (Laramide) diastrophism the thick Cretaceous sediments of the trough were overthrust against the flank of the platform; after uplift and erosion of upper Cretaceous sedimentary rocks, late Eocene and early Oligocene eruptions covered most of the area with the volcanic rocks of the Vieja Group (WILSON *et al.*, 1968). The Vieja Group consists of nine named formations (DEFORD, 1958), from bottom to top the Jeff Conglomerate, Gill Breccia, Colmena Tuff, Buckshot Ignimbrite, Chambers Tuff, Bracks Rhyolite, Capote Mountain Tuff, Brite Ignimbrite (now considered part of the widespread Mitchell Mesa Rhyolite), and Petan Basalt. The rocks subsequently have been block faulted, following the general trend of the Basin and Range faulting of the late Tertiary, and carved by erosion to create a modern topography of steplike mountain slopes with extrusive rocks capping prominent ridgecrests.

On the north the Vieja Group interfingers with the Garren Group in the Van Horn Mountains. A tuff of the Garren Group in the Indio Mountains in southeastern Hudspeth County has yielded land snail fossils identified as the genus *Humboldtiana* Ihering, 1892 (UNDERWOOD & WILSON, 1974). Species of *Humboldtiana* today live in the mountains bordering the Mexican Plateau and the mountains of the Big Bend region of Texas (BURCH & THOMPSON, 1957; BEQUAERT & MILLER, 1973).

Well-preserved land gastropod fossils from the Colmena Tuff and Chambers Tuff, collected by John Andrew Wilson and parties from the University of Texas, include large snails readily identifiable as belonging to the genus *Lysinoe* Adams & Adams, 1855. The only previous Tertiary fossil record of *Lysinoe* is a tentative identification by GARDNER (1945) in the Eocene of northeastern Mexico. The species, here described as new, shows remarkable similarity to the Holocene *Lysinoe ghiesbreghtii* (Nyst, 1841) of the Mexican state of Chiapas, Guatemala, Honduras, and El Salvador, and provides a basis for interpreting the paleoecology and paleoclimate of these parts of the Vieja Group.

Also present in the Colmena Tuff is a species of *Polymita* Beck, 1837, a genus confined at the present day to eastern Cuba and having no other Tertiary fossil record. The Chambers Tuff has yielded two species here assigned to *Pleurodonte* Fischer von Waldheim, 1807, a genus now confined to Jamaica and the Lesser Antilles, and a species of *Xerarionta*, similar to present-day forms from Baja California. Samples from the Devil's Graveyard Formation in the Agua Fria-Buck Hill area, Brewster County, include *Lysinoe* and a low-spined, lenticular form tentatively assigned to the Camaenidae.

The following abbreviations are used: CAS, Department of Invertebrate Zoology, California Academy of Sciences, San Francisco; Ma (Mega-annum), 10<sup>6</sup> years (before present); TMM, Vertebrate Paleontology Laboratory,

Texas Memorial Museum, University of Texas, Austin; UCMP, Museum of Paleontology, University of California, Berkeley; USGS, United States Geological Survey; USNM, Division of Paleobiology, United States National Museum of Natural History, Smithsonian Institution.

Specimen numbers of TMM consist of a five-digit locality number, a hyphen, and the specimen number from that locality, *e.g.*, 40276-16. Detailed descriptions of localities are on file at the Vertebrate Paleontology Laboratory, Texas Memorial Museum, The University of Texas at Austin. Devil's Graveyard Formation and Bandera Mesa Member are manuscript names from STEVENS *et al.* (in press) and are reserved by the Geologic Names Committee, U.S. Geological Survey.

In the species descriptions, whorls are counted by the method of PILSBRY (1939, fig. B). Shell height is measured parallel to the axis of coiling; diameter is the greatest diameter perpendicular to the axis of coiling. Both measurements exclude the expanded lip of mature specimens.

## SYSTEMATIC PALEONTOLOGY

### Class Gastropoda

#### Subclass Pulmonata

#### Order Sigmurethra

#### Superfamily Helicacea

#### Family HELMINTHOGLYPTIDAE

#### *Lysinoe* Adams & Adams

*Aglaja* ALBERS, 1850:107. *Non* Renier, 1807, *non* Eschscholtz, 1825.

*Lysinoe* ADAMS & ADAMS, 1855:203. MARTENS, 1890-1901: 145-147. PILSBRY, 1895:191-192. ZILCH, 1960:652.

*Odontura* FISCHER & CROSSE, 1870:211, 242. *Non* Rambur, 1838.

*Prionodontura* H. FISCHER, 1899:304.

*Aglaja* Albers, auctt., invalid emendation.

Type-species: *Helix ghiesbreghtii* Nyst, 1841.

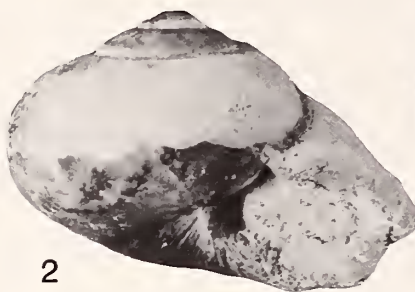
**Generic diagnosis:** Shell large, depressed-globose, with low spire; whorls convex, hirsute, brown with distinct banding; body whorl rounded, umbilicate; aperture oblique, lunate; lip dilated and somewhat reflected; columellar margin spread out by callus (ZILCH, 1960, translation).

The modern range of *Lysinoe* includes parts of Guatemala, Honduras, El Salvador, and the Mexican state of Chiapas. Three species are recognized: *L. ghiesbreghtii*, *L. eximia* (Pfeiffer, 1844), and *L. starretti* Thompson, 1963. The ranges of the latter two species are not well known. *Lysinoe ghiesbreghtii* is a large, conspicuous snail, gathered for food by the native peoples of Guatemala and Chiapas (MARTENS, 1890-1901; D. E. Breedlove, personal communication).

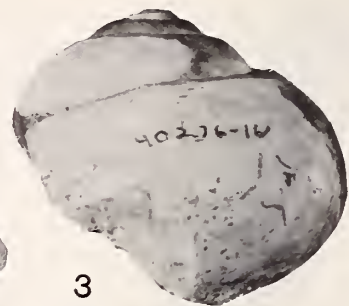
The only species originally included in *Aglaja* Albers, 1850, was *Helix ghiesbreghtii*. *Lysinoe* was proposed explicitly as a replacement name for *Aglaja* [*sic*] Albers, *non* Renier, and therefore takes the same type-species. A later



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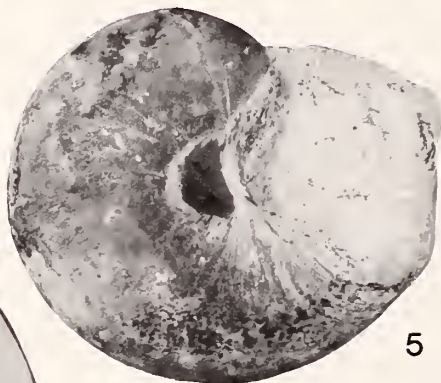
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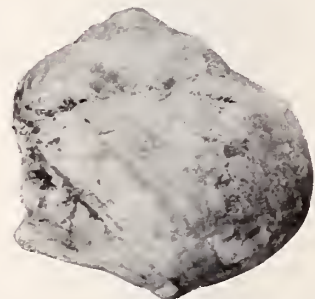
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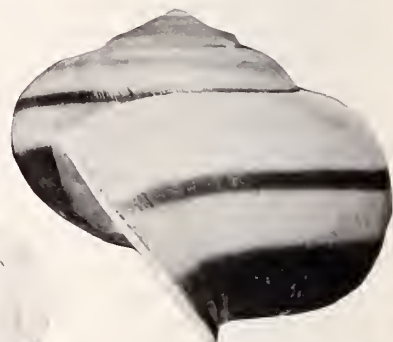
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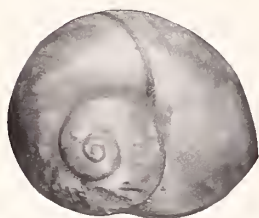
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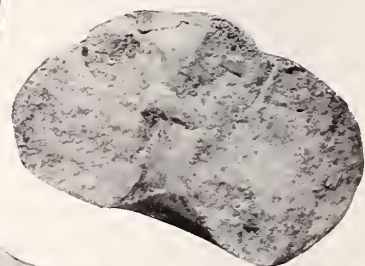
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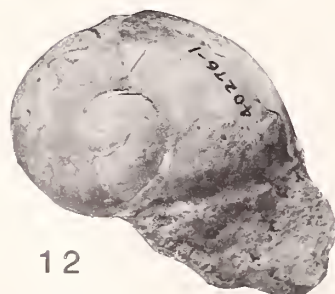
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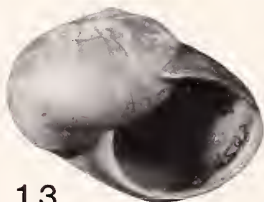
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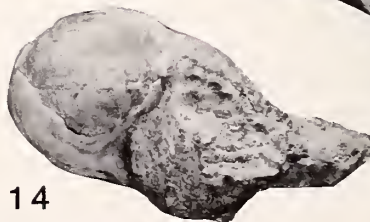
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designation (ALBERS, 1860) of *Helix audouinii* Orbigny, 1835, as type-species of *Aglaja* is invalid. Opinion 427 of the International Commission on Zoological Nomenclature rejected *Aglaja* [sic] Renier, 1804, for nomenclatorial purposes but reserved *Aglaja* Renier, 1807, for further consideration. *Priodontura* H. Fischer, 1899, was proposed as a replacement name for the preoccupied *Odon-tura* P. Fischer & Crosse.

*Lysinoe breedlovei* Roth, spec. nov.

(Figures 1-3, 5, 6, 11, 15)

"*Helix*" sp., GARDNER, 1945:18, 167; pl. 18, figs. 1-3.

[?] *Lysinoe*, GARDNER, 1945:177.

*Helix leidyi* Hall & Meek, PAMPE, 1974:292-293 (in part), pl. 1, figs. 1-7. *Non* Hall & Meek, 1855:394.

*Oreohelix grangeri* Cockerell & Henderson, PAMPE, 1974: 293, pl. 2, figs. 11, 12. *Non* Cockerell & Henderson, 1912:231.

**Diagnosis:** *Lysinoe* with depressed-trochoid shell, about 4.75 whorls, irregular papillation, large, funicular umbilicus with circumumbilical ridge, narrowly shouldered whorls, and greatest width below middle of body whorl.

**Description of holotype:** Shell moderately thin, depressed-trochoid, broadly umbilicate; umbilicus funicular, contained about 6.7 times in diameter. Spire profile faintly convex; whorls of spire convex, narrowly, roundly shouldered, suture impressed. Embryonic whorls apparently about 1.5, with weak radial ribbing and a few scattered papillae, pitted by erosion. Neanic whorls with low, irregular, retractive growth rugae of varying sizes, combined on early whorls with low granulose vermiculation generally trending parallel to rugae. Rugae thickened, curved backward, and somewhat bunched below suture. From about third whorl on, also with discrete papillae, most dense on upper 1/3 of body whorl, usually irregularly spaced but in some places tending to fall in forwardly descending series. Traces of nearly obsolete spiral striation present above suture on some whorls of spire. Body whorl narrowly, roundly shouldered, widest below middle of whorl, somewhat compressed above and below periphery. Base acuminate, with distinct ridge around umbilicus. Growth rugae strong inside umbilicus; papillae sparingly

present. Last whorl slowly descending for last 1/4 turn behind lip. Aperture subquadrate, markedly oblique, at angle of 45° to axis of coiling; lip expanded and reflected. Parietal wall thickly calloused. Diameter 59.2 mm, height 40.4 mm, diameter of umbilicus 8.9 mm; whorls 4.75.

**Type material:** **Holotype:** TMM 40276-16; *Texas:* Presidio County: mouth of Capote Creek north of Candelaria. J. A. Wilson *et al.* coll., 28 June 1964. Colmena Tuff, Vieja Group. **Paratypes (4):** TMM 40276-18A, 40276-18B, 40276-28, 40276-29, same locality as holotype.

**Referred material:** TMM 31281-15 (1 specimen), 31281-20 (2), 31281-25 (1), 31281-28 (1), 31281-31 (1), 31281-35 (3), 31281-41 (1), 31281-42 (1). Presidio County: north of Capote Creek, Candelaria area. J. A. Wilson *et al.* coll., various dates between August 1960 and July 1962. Colmena Tuff.

TMM 40276-5 (1 specimen, *cf. L. breedlovei*). Presidio County: mouth of Capote Creek. J. A. Wilson coll., 7 October 1961. Colmena Tuff.

UCMP B-1362 (6 specimens, internal molds). Presidio County: 3 mi (4.8 km) north of Candelaria on north and south sides of mouth of Capote Creek; dark red-brown tuff with numerous boulder conglomerate lenses; gastropods in tuff about 70-90 ft (21-27 m) above base of Tertiary section. J. A. Wilson coll. Colmena Tuff.

TMM 41211-1 (1 specimen, figured by PAMPE, 1974, pl. 1, figs. 4, 5), 41211-2 (1). Presidio County: 0.5 mi (0.8 km) south of where road from Middleton's to Adobe Spring leaves Rooney Red Tuff Lentil. J. A. Wilson coll., 17 June 1968. Chambers Tuff, Vieja Group.

TMM 41216-5 (1 specimen). Presidio County: Capote Falls Ranch. J. A. Wilson *et al.* coll., 18 June 1968. Chambers Tuff.

TMM 41579-2 (1 specimen). Brewster County: Alamo de Cesario Creek. M. S. Stevens coll., 11 June 1973. Unnamed lower member, Devil's Graveyard Formation.

TMM 41672-22 (5 specimens). Brewster County: Purple Bench. J. A. Wilson *et al.* coll., 28 June 1974. Devil's Graveyard Formation.

TMM 41715-3 (1 specimen). Brewster County: North Fork of Alamo de Cesario Creek. M. S. Stevens coll., 18 June 1974. Skyline Channels, base of Bandera Mesa Member, Devil's Graveyard Formation.

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Explanation of Figures 1 to 14

Figures 1, 2, 3, 5, 6, and 11. *Lysinoe breedlovei* spec. nov.

Figures 1, 2, 3, and 5, holotype, TMM 40276-16, top, front, lateral, and basal views; greater diameter 59.2 mm. Figure 6, referred specimen, TMM 31281-41, lateral view; diameter 41.2 mm. Figure 11, referred specimen, TMM 31281-42, cross-section; diameter 34.8 mm.

Figure 4. *Pleurodonte (Pleurodonte) wilsoni* spec. nov., referred specimen, TMM 40206-8; diameter 22.0 mm.

Figures 7, 8, and 10. *Lysinoe ghiesbreghtii* (Nyst, 1841), Holocene, near San Cristobal de las Casas, Chiapas, Mexico, CAS 045384, top, lateral, and basal views; greater diameter 61.5 mm.

Figures 9 and 13. *Polymita picta* (Born, 1780), Holocene, Mesa de Ovando, Oriente Province, Cuba, CAS 045385, top and front views; specimen coated for photographing; greater diameter 34.0 mm.

Figures 12 and 14. *Polymita texana* spec. nov., holotype, TMM 40276-1, top and front views; greater diameter 38.5 mm.

TMM 42019-19 (1 specimen). Brewster County: Red Hill, east side, same level as Balanced Rock, Coffee Cup Ranch. M. S. Stevens coll., 21 June 1977. Devil's Graveyard Formation.

TMM 42151-5 (3 specimens). Brewster County: South of Stone Corral. M. S. Stevens coll., 16 June 1977. Cotter Channels, Bandera Mesa Member, Devil's Graveyard Formation.

I have not personally examined specimen TMM 41578-3 from the "Skyline Red Ss." (=Devil's Graveyard Formation) figured by PAMPE (1974, pl. 1, figs. 1-3; as "*Helix leidyi*") but from the illustration it is clearly *L. breedlovei*.

**Additional description:** Most of the paratype and referred material agrees in character with the holotype. A referred specimen from locality TMM 31281 shows better than the holotype the extent to which the peristome may turn outward at maturity (Figure 6). Some specimens have been compressed dorsoventrally during preservation; these show an artificially emphasized peripheral angulation. Others have been compressed or skewed laterally. Post-mortem changes aside, there seems to have been some variation in height of spire and degree of depression of the body whorl. A cross-section (Figure 11) shows that the axis is perforate throughout growth and that the circum-umbilical ridge is more acute on the early whorls.

The shell structure of *Lysinoe ghiesbreghtii* consists of (1) a thin inner lining probably of complex-prismatic structure (terminology after MACCLINTOCK, 1967); (2) a thick crossed-lamellar layer with first-order lamellae parallel to growth lines, intertonguing with (3) a second, equally thick, crossed-lamellar layer with first-order lamellae oriented at right angles to the first and parallel to the direction of growth. Fracture sections on the inner lip and body whorl of the holotype of *L. breedlovei* show that, although the shell has recrystallized, these three basic structural layers were originally present.

Referred specimen TMM 42019-19 shows a pronounced thickening and subsequent discordance of growth rugae at the 1.5-whorl stage. This appears to represent the change from embryonic to neanic shell growth.

One specimen, TMM 40276-5 (Figure 15), is exceptionally large. Although missing three quarters of the fourth whorl, the remaining internal mold is 81.2 mm in greatest diameter. The original diameter was probably in excess of 95 mm. The axis is perforate and the whorl cross-section like that of other specimens at hand. A small amount of recrystallized shell remaining around the axis shows shell layers of the same proportions as the holotype of *L. breedlovei*.

**Remarks:** *Lysinoe breedlovei* closely resembles the Holocene *Lysinoe ghiesbreghtii* (Nyst) (Figures 7, 8, 10) in size, general proportions, rate of augmentation of the whorls, and shape of aperture and umbilicus. The angle of obliquity of the aperture, in relation to the coiling axis,

is about 40° in *L. ghiesbreghtii*. The umbilicus of *L. breedlovei* is wider (Figure 5) and the circum-umbilical ridge of the base more pronounced. The body whorl of *L. ghiesbreghtii* is more tumid, with the widest part being near the middle, rather than below it as in *L. breedlovei*. In *L. breedlovei* the last whorl increases its rate of descent along the coiling axis slowly over the last ¼ turn (Figures 3, 6), whereas in *L. ghiesbreghtii* there is a sharp downturning about 1 cm behind the outer lip (Figure 8). *Lysinoe ghiesbreghtii* averages 5.1-5.25 whorls at maturity, slightly more than *L. breedlovei*.

The spire and upper part of the body whorl of *L. ghiesbreghtii* bear fine periostracal hairs arranged in diagonal series. Each of these is borne on a low, round, 0.1 mm-wide papilla reflected in the underlying calcareous layer of the shell. Papillae are present on the holotype of *L. breedlovei* but are not as regularly disposed.

*Lysinoe breedlovei* is the same species reported as "*Helix*" sp. by GARDNER (1945) from beds she assigned to the Oligocene, in Nuevo León, Mexico. Gardner herself noted the similarity to *Lysinoe*. Her figured specimen (USNM 497132) and others are internal molds with minor traces of shell remaining. They show no taxonomic characters to separate them from *L. breedlovei* of the Vieja Group. The occurrence is in a predominantly marine sequence. At one locality (USGS 14023) the species was associated with the estuarine mollusks *Erodona* and *Ampullina* and the fluviatile gastropod *Hemisinus*, indicative of permanent (not seasonal) running water. As discussed below under "Age and Correlation," the occurrence is significant for marine-nonmarine temporal correlations. The specimen from the Yegua Formation (Eocene) at Ochoa, Tamaulipas, referred to *Lysinoe* by GARDNER (1945:177) is, at this writing, temporarily unavailable for borrowing (T. R. Waller, *in litt.*, 1983) but should also be examined in this context.

The large, umbilicate land snail described as *Helix spatiosa* Meek & Hayden, 1861, from the upper Paleocene to middle or upper Eocene of the Rocky Mountain and northern Great Plains regions, discussed as the type-species of an unnamed new genus by TAYLOR (1975), differs from *L. breedlovei* in having six or more tightly coiled whorls and apical sculpture of retractive riblets like those of *Or-eohelix*.

The large *Helix hesperarche* Cockerell, 1914, from an unknown locality but thought to be from the Eocene of New Mexico, differs in having the whorls more tightly coiled and the umbilicus narrower (0.12 times diameter, versus 0.15-0.16 in *L. breedlovei*). HENDERSON (1935) thought he recognized "*H.*" *hesperarche* from "the O-2 Ranch, about 25 miles south of Alpine," Texas. I have not examined Henderson's specimens, but it seems likely that he had *L. breedlovei*.

PAMPE (1974), possibly taking a cue from Russell (in GOLDICH & ELMS, 1949), referred large specimens of *L. breedlovei* to *Helix leidyi* Hall & Meek, 1855, and small-

er internal molds of the same species to *Oreohelix grangeri* Cockerell & Henderson, 1912. "*Helix*" *leidyi* from the White River Group of South Dakota and Nebraska is a globose form with narrow umbilicus, not assignable to any modern genus of Helminthoglyptidae. *Oreohelix grangeri* from the lower Eocene of Bighorn Basin, Wyoming, is a depressed, carinate form that may represent young individuals of "*Helix*" *spatiosa*.

**Etymology:** The species is named for Dennis E. Breedlove, Curator of Botany, California Academy of Sciences, and expert on the flora of Chiapas, in recognition of his personal investigations of *Lysinoe* and other Mexican mollusks.

### *Polymita* Beck

*Polymita* BECK, 1837:44. PILSBRY, 1895:187-189. TORRE Y HUERTA, 1950:7-9. MORENO, 1950:21-35. ZILCH, 1960:662.

*Oligomita* TORRE Y HUERTA, 1950:18.

Type-species: *Helix picta* Born, 1780.

**Generic diagnosis:** "Shell subglobular, brilliantly colored, rather thin but solid, imperforate; whorls few (about four), the last but little deflexed; aperture rounded, slightly lunate, the peristome simple, not expanded or reflexed except at axis, where it is reflexed and adnate over the umbilical region; axis solid" (PILSBRY, 1895:188).

The modern range of the genus is restricted to Oriente Province, eastern Cuba. The species of *Polymita* are arboreal and probably feed on epiphytic fungi and lichens (TORRE Y HUERTA, 1950).

*Polymita texana* Roth, spec. nov.

(Figures 12, 14)

**Diagnosis:** *Polymita* with large, depressed-globose shell with low spire, very rapidly enlarging body whorl, and large first nuclear whorl.

**Description of holotype:** Shell large for the genus, thin, depressed-globose, of 3.75 rapidly enlarging whorls; spire low; suture not deeply impressed. Embryonic whorls about 1.3, smooth, demarcated from neanic whorls by a weak constriction. Neanic whorls smooth, with almost obsolete, rounded growth lines and impressed radial growth rests at intervals of one half to one whorl. First neanic whorl with two prominent radial rugae right after embryonic whorls, and an impressed growth rest at first half whorl. Prominent growth rests occurring at 1.8, 2.8, and 3.3 whorls, with an internal thickening of the shell wall at each rest, followed by a sudden increase in internal whorl diameter. Periphery broadly rounded; body whorl descending slowly toward aperture, slightly constricted behind outer lip. Outer lip weakly turned outward, internally thickened by low smooth ridge along margin. Parietal wall simple, smooth; inner lip with thin secondary layer

of smooth callus reflected over columella. Major diameter 38.5 mm, minor diameter (incomplete) 27.2 mm, height 25.9 mm.

**Type material: Holotype:** TMM 40276-1. Texas: Presidio County: mouth of Capote Creek north of Candelaria. Bill Brannan coll., 1957. Colmena Tuff, Vieja Group.

**Remarks:** The rapid rate of whorl expansion of the few-whorled, subglobose shell, the steplike enlargement of whorl diameter after a growth rest, and the smooth secondary callus reflection over the columellar region are all distinctive characteristics of *Polymita*, and most similar to *Polymita picta* (Born) (Figures 9, 13).

The holotype (the only known specimen) is a nearly intact internal mold with pieces of shell remaining at the apex, on the outer part of the body whorl back for  $\frac{1}{3}$  turn from the outer lip, and around the columellar margin of the aperture. It differs from *P. picta* in having 0.25-0.5 whorl less (based on large specimens of *P. picta*) and a larger first nuclear whorl—1.6 mm in diameter compared to 1.25 mm for *P. picta*. The shell has been slightly distorted in preservation, but the spire probably was lower originally than the average spire of *P. picta*. The outer lip of the fossil turns out more strongly than that of *P. picta*.

The holotype is distinguishable from *Humboldtiana* by its smooth surface, without any trace of granulose or papillose sculpture or the heavy, irregular growth wrinkles characteristic of that genus. Many species of *Humboldtiana* have nuclear whorls the same size as this fossil; most have a radially wrinkled protoconch, but this fine sculpture is readily removed by erosion even in living snails. *Humboldtiana* are narrowly umbilicate. The inner lip callus of the specimen at hand is broken at the lower end and may originally have left exposed a small umbilical chink, but the part that remains extends lower on the shell and is more broadly spread onto the body whorl than in any known *Humboldtiana* species.

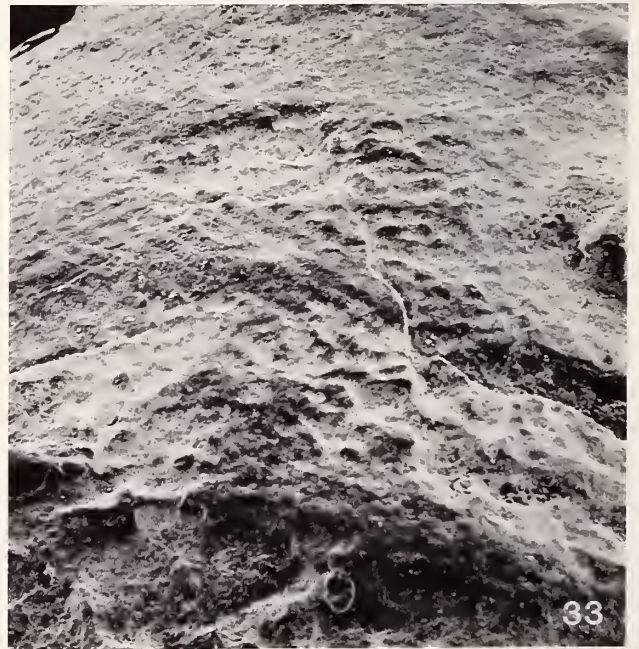
### *Xerarionta* Pilsbry

*Xerarionta* PILSBRY, 1913:382. PILSBRY, 1939:214-215.

Type-species: *Arionta veitchii* Tryon, 1866, ex Newcomb MS (= *Xerarionta levis canescens* [Adams & Reeve, 1848]).

**Generic diagnosis:** "Rather capacious, globose-conic or depressed-globose shells, perforate or closed, copiously variegated or sometimes white; the embryonic  $1\frac{1}{2}$  whorls with radial sculpture or nearly smooth; peristome moderately or scarcely expanded, shortly dilated at the axial insertion" (PILSBRY, 1939:214).

Formerly considered a subgenus of *Micrarionta* Ancey, 1880, *Xerarionta* was elevated to generic rank by MILLER (1981). Its modern range includes the regions of Baja California that are influenced by Pacific Ocean fogs (MILLER, 1973; SMITH *et al.*, in preparation), the southern California Channel Islands, and the adjacent mainland.



*Xerarionta areolata* occurs as fossils of Pleistocene or early Holocene age on Isla Monserrate, Isla Espíritu Santo, and the nearby Baja California mainland, but there is no prior Tertiary record of the genus.

*Xerarionta waltmilleri* Roth, spec. nov.

(Figures 16, 17, 33)

*Helix leidyi* Hall & Meek, PAMPE, 1974:292-293 (in part), pl. 1, figs. 8-10. *Non* HALL & MEEK, 1855:394.

[?] *Humboldtiana* UNDERWOOD & WILSON, 1974:596-597, text-fig. 2.

**Diagnosis:** *Xerarionta* with depressed-globose shell, umbilicus filled by impressed callus pad, tumid body whorl, and fine, even, overall granulation with granules aligning diagonally.

**Description of holotype:** Shell large for the genus, depressed-globose, imperforate. Spire profile slightly convex; whorls of spire flattish to weakly rounded; suture scarcely impressed until penultimate whorl. Embryonic whorls not clearly demarcated from neanic whorls. Neanic whorls sculptured with fine, even, overall granulation (best seen by low-angle light), the granules close, aligning in diagonal series; and moderately prominent, retractive growth rugae. Granulation weaker on base and perhaps also on upper part of whorl below suture; locally appearing as network of minute, diagonal, incised grooves. Body whorl tumid, moderately compressed above the well-rounded periphery. Base inflated, umbilical region not strongly indented. Last whorl slowly descending for last  $\frac{1}{2}$  turn and weakly constricted just behind lip. Aperture semilunate, oblique; lip narrowly expanded, reflected at base. With impressed callus pad filling umbilical region. Parietal wall with thin, simple callousing. Diameter 25.9 mm, height 19.8 mm; whorls 5.1.

**Type material: Holotype:** TMM 40209-1006; *Texas:* Presidio County: Reeves Bone Bed, 96 Ranch. J. A. Wilson *et al.* coll., December 1966. Upper part of Chambers Tuff, Vieja Group. **Paratypes (17):** TMM 40209-502A, 40209-1007 through 40209-1022, same locality as holotype.

**Additional description:** The type lot consists of internal molds ranging from poor to moderately good preservation. The holotype retains considerable original shell. The regular granulose sculpture that suggests assignment to *Xerarionta* is preserved on the body whorl from right behind the aperture to about  $\frac{1}{3}$  turn back (Figure 33) and at several places on the penult. A strongly compressed paratype also shows the same sculpture extending across the base almost to the umbilical region.

**Remarks:** The relatively symmetrical, globose shape of the body whorl, without sharp descent along the axis of coiling, is suggestive of *Xerarionta* and most plainly seen in *X. areolata* (Pfeiffer, 1845) (Figure 18). In *Humboldtiana* the body whorl expands at a greater rate and slopes obliquely down and away from the coiling axis. The aperture is more effuse. Granulose sculpture is present in some species of *Humboldtiana* but is of a different type: the granules tend to align along growth lines and often merge with the growth rugae. They are often irregular in size and only rarely produce anything like the fine, even, overall, diagonally trending fabric of the surface of *X. waltmilleri*.

Granulose sculpture also occurs in *Pleurodonte* (*Dentellaria*), but here also the granules are aligned primarily parallel to growth lines. The globose shape of *X. waltmilleri* and its simple, weakly deflected aperture distinguish it from *Pleurodonte* or any similar camaenid genera.

The microsculpture in *Xerarionta* is varied, from smooth with weak wrinkles of growth (*X. areolata*) to deeply cut

Explanation of Figures 15 to 33

Figure 15. *Cf. Lysinoe breedlovei* spec. nov., referred specimen, TMM 40276-5, top view; greatest diameter 81.2 mm.

Figures 16, 17, and 33. *Xerarionta waltmilleri* spec. nov., holotype, TMM 40209-1006. Figures 16 and 17, top and front views; greater diameter 25.9 mm. Figure 33, SEM photograph of diagonal microsculpture obliquely crossing growth rugae (curved horizontal ridges) on body whorl behind outer lip,  $\times 20.7$ .

Figure 18. *Xerarionta areolata* (Pfeiffer, 1845), Holocene, shore of Bahía Magdalena, Baja California Sur, Mexico, CAS 045386; diameter 25.6 mm.

Figures 19, 20, 23, 24, and 25. *Pleurodonte* (*Pleurodonte*) *wilsoni* spec. nov. Figures 19 and 20, holotype, TMM 40840-50, top and basal views; greater diameter 24.5 mm. Figures 23 to 25, paratype, TMM 40840-52, top, basal, and lateral views; greater diameter 24.1 mm.

Figures 21 and 22. *Pleurodonte* (*Dentellaria*)(?) species, referred

specimen, TMM 40206-56, top and basal views; greater diameter 17.7 mm.

Figure 26. *Pleurodonte* (*Pleurodonte*) *isabella* (Ferussac, 1821), Holocene, St. John's churchyard, Barbados, CAS 045388; greater diameter 23.6 mm.

Figures 27, 28. *Pleurodonte* (*Dentellaria*) *anomala* (Pfeiffer, 1848), Holocene, Jamaica, CAS 045387; greater diameter 22.3 mm.

Figures 29, 30, and 31. Camaenid, genus and species indet., referred specimen, TMM 41579-49, top, front, and basal views; greater diameter 16.1 mm.

Figure 32. *Xerarionta redimita* (Binney, 1858), Holocene, between Horse and Red Rock canyons, San Clemente Island, California, CAS 045389; SEM photograph of diagonal microsculpture on lower part of body whorl behind outer lip,  $\times 22.0$ . Specimens in Figures 16 to 33 have been coated for photographing.



by incised spiral grooves (*X. intercosa* [Binney, 1857], *X. pandorae* [Forbes, 1850]). The only extant species with minute overall granulation are *X. redimita* (Binney, 1858) (Figure 32) from San Clemente Island, and *X. kellettii* (Forbes, 1850) from Santa Catalina Island, California, and the adjacent mainland. The microsculpture of *X. kellettii* is often faint or reduced to minute diagonal grooves between growth lines, especially on the base. A small amount of granulation can sometimes be seen on the first neanic whorl of *X. areolata*; no diagonal trend is evident. *Xerarionta levis* (Pfeiffer, 1845) has granulose wrinkling upon the first and second neanic whorls, much more irregular than that of *X. redimita* and *X. kellettii*.

*Xerarionta waltmilleri* may be the same species reported as *Humboldtiana* from the Garren Group, Hudspeth County (UNDERWOOD & WILSON, 1974). As of this writing, those specimens are temporarily unavailable for borrowing (T. R. Waller, *in litt.*, 1983) but should be re-examined later.

**Etymology:** The species is named for Walter B. Miller of the University of Arizona, in recognition of his many contributions on the Helminthoglyptidae and other mollusks of the American Southwest.

Superfamily CAMAENACEA  
Family CAMAENIDAE

BISHOP (1979) summarized the Tertiary species from North America that have been assigned to the Camaenidae. A species of *Caracolus* Montfort, 1810, *C. aquilonaris* Bishop, 1979, has been recognized in the upper Oligocene Whitney Member of the Brule Formation, White River Group, Sheridan County, Nebraska. SOLEM (1978) commented on the similarity between *Hodopoeus crassus* Pilsbry & Cockerell, 1945 (described from an unknown locality but thought to be from the Eocene of the southwestern United States), and several species of *Iso-meria* Albers, 1850. COCKERELL (1914) suggested a relationship between his *Helix hesperarche* and West Indian Camaenidae; the holotype, an internal mold, lacks the apertural characters that could confirm this placement.

*Pleurodonte* Fischer von Waldheim

*Pleurodonte* FISCHER VON WALDHEIM, 1807:229. WURTZ, 1955:119-120. ZILCH, 1960:601.

Type-species: *Helix lychnuchus* Müller, 1774.

Subgenus *Pleurodonte*, *sensu stricto*

**Subgeneric diagnosis:** Shell solid, globose or depressed, with low, convex, conical spire; body whorl rounded or angulate, imperforate; aperture oblique, broader than high; lip dilated and strongly thickened, mostly toothed, the limbs connected by a more or less robust parietal callus, which sometimes is also toothed (ZILCH, 1960, translation).

The modern range of *Pleurodonte*, *sensu stricto* is limited to the Lesser Antilles. One or more other species occur in

the Miocene of Carriacou, Grenadines (JUNG, 1971). *Pleurodontites* Pilsbry, 1939, from the Tampa Limestone (lower Miocene) is probably closely related. "*Pleurodonte*" *eohippina* Cockerell, 1915, from the Sand Coulee Beds, Eocene (Wasatchian), Clarks Fork Basin, Wyoming, was regarded as a helicid prosobranch and made the type-species of a new genus, *Eohippitychia*, by BISHOP (1980), but the available information on the unique specimen is not adequate to permit critical commentary on its ordinal placement (SOLEM, *in press*).

BISHOP (1979) suggested that antecedents to *Pleurodonte* were once widespread throughout the Antilles but that *Pleurodonte* has become extinct on Cuba, Hispaniola, and Puerto Rico. The new species next described and the following one show that *Pleurodonte* was already differentiated in North America by the late Eocene and that at least two types of shell form were present at that time.

*Pleurodonte* (*Pleurodonte*) *wilsoni* Roth, *spec. nov.*

(Figures 4, 19, 20, 23-25)

*Polygyra veternior* (Cockerell), PAMPE, 1974:293-294 (*in part*), pl. 2, figs. 5-7. *Non Helix veterna veternior* COCKERELL, 1915:117.

**Diagnosis:** *Pleurodonte* with depressed, tumid, imperforate shell, 4.7-5.1 whorls, periphery rounded to angular, body whorl sharply deflected downward behind aperture, lip thickened but not dentate.

**Description:** Shell small for the subgenus, depressed, imperforate. Spire low, obtuse; spire profile convex; suture lightly impressed, more deeply incised around last 0.5-0.75 whorl. Embryonic whorls not well differentiated from neanic whorls. Surface apparently smooth, with blunt, indistinct growth rugae. Body whorl narrow, with rounded or subangular periphery; base compressed, smooth, flattish. Last whorl turning sharply downward behind aperture. Aperture broadly crescentic, very oblique, at angle of 60-70° to axis of coiling; lip expanded and strongly thickened but not dentate; parietal wall callused, without teeth. Diameter of holotype 24.5 mm, height 14.2 mm; whorls 4.8.

**Type material: Holotype:** TMM 40840-50; *Texas:* Presidio County: Chalk Gap Draw. J. A. Wilson coll., June 1965. Upper part of Chambers Tuff, Vieja Group. **Paratypes (8):** TMM 40840-52 (1), 40840-53 (7), same locality as holotype.

**Referred material:** TMM 40206-8 (1 specimen), 40206-54 (1), 40206-55 (1). Presidio County: Northwest of Big Cliff. J. A. Wilson coll., 19 June 1960. Lower part of Chambers Tuff.

TMM 40209-502 (4 specimens; one figured by PAMPE, 1974, pl. 2, figs. 5-7, as "*Polygyra veternior*"; associated with Little Egypt local fauna, not Candelaria local fauna as stated). Presidio County: Reeves Bone Bed, 96 Ranch.

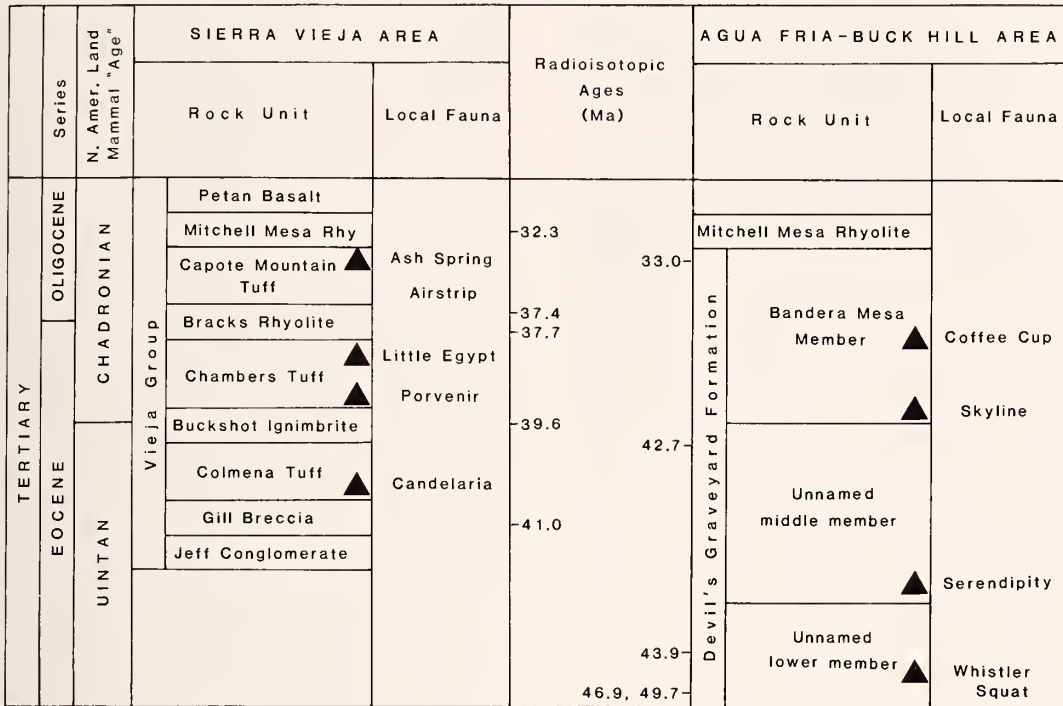


Figure 34

Correlation of rock units, radioisotopic ages, and mammal-based local faunas in Sierra Vieja and Agua Fria-Buck Hill areas. Filled triangles indicate sources of land mollusks reported in this study. Radioisotopic ages from WILSON *et al.* (1968) and WILSON (1978, and personal communication, 1983), corrected for new decay and abundance constants (DALRYMPLE, 1979).

J. A. Wilson *et al.* coll., 1966. Upper part of Chambers Tuff.

TMM 40283-82 (10 specimens). Jeff Davis County: Ash Spring. J. A. Wilson coll., 16 June 1965. Vieja Group, undifferentiated.

**Additional description:** The description given above is composite, because no single specimen in the type lot shows all the characters. All specimens are internal molds, with scraps of recrystallized shell remaining, mainly in the suture but occasionally around the aperture or on the spire. The major variation is in the shape of the periphery, which ranges from evenly rounded to subangular in the type lot. The referred material from the Big Cliff locality (TMM 40206) is lenticular (Figure 4) with a distinctly angled periphery. Material from the undifferentiated Vieja Group at Ash Spring is rounded, with only a hint of angulation showing on some specimens. Comparable variability is known in some modern species of *Pleurodonte*, for example *P. acuta* (Lamarck) illustrated by PILSBRY (1889-1890, pl. 26). It is also possible that sedimentary compaction tends to emphasize the peripheral angulation, as in *Lysi-noe breedlovei*.

Representative "mature" specimens (those with thickened lip) measure:

Locality	Diameter	Height	No. of whorls
TMM 40840	24.1 mm	13.6 mm	4.75
	23.5	13.2	4.75
TMM 40206	21.7	12.1	5.1
TMM 40209	20.5	12.3	4.75
	19.2	12.6	5.1
TMM 40283	24.1	17.0	5.0
	23.6	13.0	4.7
	23.1	14.6	5.1
	23.0	14.5	5+
	22.8	14.2	4.9
	22.2	14.3	4.7

Several specimens show a slight upward constriction of the base of the last whorl directly behind the aperture. This is a relatively common feature in *Pleurodonte* and other genera of American Camaenidae.

**Remarks:** *Pleurodonte wilsoni* resembles the Holocene *Pleurodonte isabella* (Ferussac, 1821) (Figure 26) and several other related species. The group was most comprehensively reviewed, at least for shell characters, by PILSBRY (1889-1890, 1893-1895). The spire of *P. isabella* is more domelike and the suture scarcely impressed at all until the last whorl. An irregular or denticulate ridge runs along

the basal lip of *P. isabella*; there is evidently no such ridge in *P. wilsoni*. *Pleurodonte lehneri* (Trechmann, 1935) from the Miocene of Carriacou, Grenadines, is also similar but has a strong, prominent tooth in the middle of the upper lip and two sometimes poorly developed denticles on the basal lip. Its spire is often, although not invariably, higher, and more domelike. Most specimens are less than 20 mm in diameter. However, the holotype of "*Helix*" *carriacouensis* (Trechmann, 1935), synonymized with *P. lehneri* by JUNG (1971), is 24.6 mm wide.

*Helix veterna veterrior* Cockerell, 1915, from the lower Eocene of Wyoming, is a more globose form, apparently known from immature specimens only. It does not have the oblique aperture, descending last whorl, upwardly constricted base, or any other characters that would permit it to be associated with *P. wilsoni*.

**Etymology:** The species is named for John Andrew Wilson, who has contributed more than anyone else to the knowledge of Vieja Group paleontology.

#### Subgenus *Dentellaria* Schumacher

*Dentellaria* SCHUMACHER, 1817:69, 230. WURTZ, 1955:125–128. ZILCH, 1960:602.

*Lucerna* "Humphrey" SWAINSON, 1840:328. *Non* Willoughby, 1816.

Type-species: *Helix sinuata* Müller, 1774.

**Subgeneric diagnosis:** Shell solid, depressed-globose to lenticular; 4.5–6 whorls, finely and densely granulose; body whorl rounded or carinate, descending toward the aperture, umbilicate or imperforate; aperture very oblique, broader than high; lip broadly reflected; basal lip with 0–5 teeth, the limbs connected by a toothless parietal callus (ZILCH, 1960, translation).

WURTZ (1955) found the anatomical differences between *Dentellaria* and *Pleurodonte*, *sensu stricto* to be minor and kept the two taxa separate (as infrasubgeneric "sections") solely on conchological grounds.

The modern range of *Dentellaria* is limited to Jamaica. Two species occur at Bowden, Jamaica, in beds assigned a Pliocene age (BISHOP, 1979). SOLEM (1978) assigned *Kanabohelix kanabensis* (White, 1876), from the upper Cretaceous of Utah, to the Camaenidae; he remarked on its similarities to *Dentellaria*, but kept the two genera separate. BISHOP (1980) considered *K. kanabensis* a helicoid prosobranch on the basis of the form of its palatal barriers; but because it retains internal whorl partitions, SOLEM (in press) restored it to the Camaenidae.

#### *Pleurodonte* (*Dentellaria*)(?) species

(Figures 21, 22)

**Description:** Shell depressed, broadly umbilicate, with 3.8 whorls preserved at a diameter of 17.7 mm; nearly flat-spined, with first whorl apparently depressed slightly below level of second; suture distinct, shell wall thickened on either side. Periphery rounded, widest above middle;

last preserved whorl narrow, cross-section taller than broad; base narrowed, with acuminate circum-umbilical ridge; umbilicus large, steep-sided. Apertural characters not preserved (specimen immature).

**Referred material:** TMM 40206-56 (1 specimen). *Texas:* Presidio County: Northwest of Big Cliff. J. A. Wilson *et al.* coll., 19 June 1960. Lower part of Chambers Tuff, Vieja Group.

**Remarks:** The single specimen at hand is an internal mold with traces of thoroughly recrystallized shell remaining at the suture, on the parietal wall, and around the umbilicus. Although the specimen is obviously immature and shows none of the characters of an adult peristome, it is similar to the Jamaican *Pleurodonte* (*Dentellaria*) *anomala* (Pfeiffer, 1848) (Figures 27, 28). The almost flat spire with depressed first whorl and the narrow whorl cross-section are similar in both. At the level of the suture, the shell of *P. anomala* is thickened by a small spiral carina to which the summit of the subsequent whorl is appressed. The shell of the fossil is thickened (although not carinate) at the same position, and the shell remaining outboard of the suture is also quite thick. *Pleurodonte anomala* has even, overall granulation. The only section of shell on the fossil not too recrystallized to show the original surface is around the umbilicus inside the last whorl; this is smooth with faintly raised growth lines. The umbilicus is more steeply walled and the base more acuminate than in *P. anomala*.

#### Camaenid, genus and species indet.

(Figures 29–31)

*Polygyra veterrior* (Cockerell), PAMPE, 1974:293–294 (in part), pl. 2, figs. 8–10. *Non Helix veterna veterrior* COCKERELL, 1915:117.

**Description:** Shell lenticular, umbilicate, of 5.1 whorls. Spire low, whorls little inflated; suture moderately impressed, distinct. Embryonic whorls not well differentiated from neanic whorls. Whorls narrowly, obtusely shouldered; periphery rounded-subangulate, widest part above middle of penult but descending below middle on body whorl. Preserved sculpture of a few low, irregular, forwardly bowed, retractive growth rugae. Body whorl with flat shoulder, not markedly descending until 0.1 whorl behind aperture, where it turns down at angle of about 30° from horizontal. Base compressed, constricted upward behind aperture; umbilicus 0.14 times diameter. Aperture broadly ovate, very oblique, at angle of 60–70° to axis of coiling; lip simple, turned outward but little thickened, encroaching on umbilicus but not appressed at base. Parietal wall with thick wash of callus but no denticulation. Diameter 16.1 mm, height 8.8 mm, diameter of umbilicus 2.4 mm.

**Referred material:** TMM 41579-49 (1 specimen). *Texas:* Brewster County: Alamo de Cesario Creek. M. S. Ste-

vens coll., 11 June 1973. Unnamed lower member, Devil's Graveyard Formation.

**Remarks:** The single specimen consists of thoroughly recrystallized shell around a light, yellowish-gray, tuffaceous siltstone matrix. Although quite well preserved, it cannot be assigned to any known genus. The lenticular shape and umbilicate base suggest *Oreohelix* Pilsbry, 1904 (Oreohelicidae) but the outward-turning lip and the sharp terminal downward deflection of the body whorl are not typically oreohelicid. In contrast, the slight upward constriction of the base behind the aperture is a feature seen in several American genera of the Camaenidae. A constriction of about the same relative magnitude occurs in several species of *Isomeria* Albers, 1850. Almost all living species of *Isomeria* are large-shelled (to a diameter of 70+ mm). The only one normally under 20 mm when adult is *I. minuta* Solem, 1966. Several species of *Labyrinthus* Beck, 1837, become adult in the 15–20 mm diameter size range, although most are larger (to 60 mm). In all modern species the basal constriction is pronounced and the aperture provided with various denticles and lamellae.

The specimen was taken with numerous specimens of a planorbid fresh-water gastropod discussed and illustrated by PAMPE (1974, pl. 2, figs. 1–4) under the name *Biomphalaria spectabilis* (Meek).

#### AGE AND CORRELATION

The type locality of *Lysinoe breedlovei*, at the mouth of Capote Creek on the Rio Grande about 2 mi (3.2 km) north of Candelaria, is the source of the Candelaria local fauna. This fauna, summarized by WILSON (1978, tables 1, 2, 14) is assigned to the Uintan North American Land Mammal "Age" (BLACK & DAWSON, 1966; WILSON *et al.*, 1968; WILSON, 1978) (Figure 34). From a study of the rodents, WOOD (1974) suggested that the Candelaria local fauna was slightly younger than the Myton local fauna of the Uinta Formation of Utah.

The Colmena Tuff is bracketed stratigraphically by radioisotopic dates based on potassium-argon analysis of sanidine concentrates. Volcanic rock from the Gill Breccia, underlying the Colmena Tuff, yielded an age determination of  $40.0 \pm 2.0$  Ma (WILSON *et al.*, 1968, figs. 1, 2, table 3; sample "0"). Corrected for the new  $^{40}\text{K}$  decay and abundance constants (DALRYMPLE, 1979) the determination is equivalent to  $41 \pm 2$  Ma. Three samples from the Buckshot Ignimbrite, which overlies the Colmena Tuff, yielded age determinations of  $35.2 \pm 2.3$  Ma,  $34.7 \pm 2.0$  Ma, and  $38.6 \pm 1.2$  Ma (WILSON *et al.*, *loc. cit.*; samples 1, 2, and 2a respectively). The latter two determinations were made from the same rock specimen; the authors give reasons for favoring the older age determination. Corrected for the new constants it sets a minimum age of around 39 Ma for the Candelaria local fauna.

In the lower part of the Chambers Tuff, *Lysinoe breedlovei*, *Pleurodonte wilsoni*, and *Pleurodonte (Dentellaria)*(?) sp. are associated with the Porvenir local fauna.

This fauna, summarized by WILSON (1978, tables 3–7, 14) is assigned to the early part of the Chadronian North American Land Mammal "Age" (WILSON *et al.*, 1968; WILSON, 1978). The fossil localities lie stratigraphically above the Buckshot Ignimbrite with its K-Ar ages as given above, and below the Bracks Rhyolite, which has yielded age determinations of 36.8 Ma (EVERNDEN *et al.*, 1964) and  $36.5 \pm 1.2$  Ma (WILSON *et al.*, 1968). Corrected for the new constants, these determinations are equivalent to 37.7 and  $37.4 \pm 1.2$  Ma.

*Pleurodonte wilsoni* and *Xerarionta waltmilleri* occur in the upper part of the Chambers Tuff, associated with the Little Egypt local fauna. This fauna, summarized by WILSON (1978, tables 8–10, 14) is also Chadronian (WILSON *et al.*, 1968; WILSON, 1978). The Bracks Rhyolite is absent in the areas where the Little Egypt local fauna occurs (Chalk Gap Draw and the Reeves Bone Bed), but a red sandstone that elsewhere lies immediately under the Bracks is present. The age of this fauna is therefore regarded as constrained by the same radioisotopic dates as the stratigraphically lower Porvenir local fauna.

*Pleurodonte wilsoni* also occurs in the undifferentiated Vieja Group at the Ash Spring locality in Jeff Davis County (loc. TMM 40283), associated with the Ash Spring local fauna. This fauna is summarized by WILSON (1978, tables 12, 14). It is regarded as Chadronian, and younger than the other local faunas of the Vieja Group based on evolutionary position of vertebrate taxa (WILSON, 1978: 27).

Correlation of units in the Agua Fria–Buck Hill area (Figure 34) is based on unpublished information supplied by J. A. Wilson (personal communication, 1983). *Lysinoe breedlovei* occurs in association with the Whistler Squat (early Uintan), Serendipity (late Uintan), Skyline, and Coffee Cup (early Chadronian) local faunas. Radioisotopic ages (corrected) of 32.3 Ma from the Mitchell Mesa Rhyolite, which overlies the Devil's Graveyard Formation, and 33.0 Ma from basalt high in the Bandera Mesa Member of the Devil's Graveyard Formation set a minimum age for the Coffee Cup local fauna. An isotopic age of 42.7 Ma from tuff in the unnamed middle member sets a maximum age for the Coffee Cup and Skyline local faunas and a minimum age for the Serendipity local fauna. Age determinations of 43.9 Ma from biotite and 46.9 and 49.7 Ma from tuff in the unnamed lower member set a maximum age for the Serendipity local fauna and bracket the Whistler Squat local fauna.

The Decade of North American Geology (DNAG) geologic time scale (PALMER, 1983) places the Eocene–Oligocene boundary at 36.6 Ma; dates between 36.6 and 40.0 Ma are classified as late Eocene. In most of the literature on Vieja Group paleontology, however, the lower limit of the Chadronian "age" and the base of the Oligocene are treated as approximately coincident (*cf.* WILSON, 1978, fig. 5). In Figure 34 the DNAG placement of the Eocene–Oligocene boundary is followed; the boundary falls at or

slightly above the stratigraphic level of the Bracks Rhyolite. Magnetostratigraphy of the Vieja Group is in agreement with these correlations (PROTHERO *et al.*, 1982).

A number of North American land mollusks are known from deposits regarded as correlative with the Colmena Tuff or the Chambers Tuff, but only a few of the occurrences have been critically analyzed. The lower part of the Sespe Formation, Ventura County, California, is of Uintan (late Eocene) age (LILLEGRAVEN, 1979) and is the source of *Helminthoglypta? stocki* Hanna, 1934. This large land snail is definitely not a *Helminthoglypta*, but its proper allocation and paleoclimatic implications are not yet known. D. W. TAYLOR (1975, and *in* ROSS, 1959 [1960]) reported three species of land snails of probable late Eocene age and three others of probable Oligocene age from the Flathead River valley, Montana-British Columbia. Early Tertiary formations of the Bozeman Group in the Three Forks Quadrangle, southwestern Montana, have yielded a diverse molluscan fauna consisting of the genera *Gastrocopta* (four species), *Pupoides* (*Ischnopupoides*) (two species), *Radiocentrum* (two species), *Polygyrella*, and *Helminthoglypta* (ROTH, *in press*). The formations range in age from probable middle or late Eocene (Uintan or earlier) to early Oligocene (Chadronian). The assemblages have a temperate aspect and suggest that a thermal stratification—latitudinal, altitudinal, or both—existed during this time. The temporal correlations, however, are mostly inferential. TAYLOR (1975, tables 18, 27, 28, 31–33, figure 3) reported land mollusks of late Eocene to Oligocene age from formations in central, southwestern, and northwestern Wyoming. The full description of these terrestrial mollusk faunas, their interrelationships, and time correlation, remain for the future. For the present it may be noted that the molluscan faunas of the northern Cordillera have little in common with those of the Vieja Group.

Based on faunal correlation with the Chambers Tuff, UNDERWOOD & WILSON (1974) assigned an age between 38 and 39 Ma to the tuff of the Garren Group in Hudspeth County, Texas, that yielded specimens of *Humboldtiana*. Vertebrate remains from the same rock sequence correlate with the Porvenir local fauna (early Chadronian) (WILSON, 1978).

The *Lysinoe breedlovei* from Nuevo León occur low in the upper of two marine sandstones containing a "Vicksburg" molluscan fauna (GARDNER, 1945). The Vicksburg Group of the Gulf Coastal Plain traditionally has been regarded as Oligocene and correlated with the Rupelian Stage of Europe (COOKE *et al.*, 1943; BERGGREN, 1971). On the recent DNAG geologic time scale (PALMER, 1983), the Rupelian Stage is entirely post-Eocene in age, younger than 36.6 Ma. The *Lysinoe* occur with *Ampullina mississippiensis* (Conrad), which is characteristic of the Mint Spring Formation of the Vicksburg Group in Mississippi and, according to Gardner, may be restricted to that horizon. A recent faunistic study (DOCKERY, 1982) adds no new information on Mint Spring interregional correlations.

## PALEOECOLOGY AND PALEOCLIMATE

Compared to that of mammals, the average rate of evolutionary change expressed in the morphology of land snails is slow. The earliest fossil land snails, from the Pennsylvanian and Permian periods, are assignable to extant families (SOLEM & YOCHELSON, 1979). Many modern genera make their first appearance in upper Cretaceous or Paleogene strata of North America, and in some cases the shells present essentially no tangible differences from those of species living today (ROTH, *in press*). If a low rate of change is assumed to extend to physiological tolerances as well—that is, if morphologic change is regarded as a fair sample of total evolutionary change—land snail fossils can be viewed with confidence as indicators of ancient environments.

At present the Rim Rock Country is part of the most arid region of Texas, with normal annual precipitation between 20 and 30 cm, most of it falling in summer. The mean annual temperature is 16.9°C, and there is a mean annual range of temperature of 19.5°C. The normal mean temperature for the coldest month is 7.2°C (U.S. Department of Commerce, 1968). The sparse vegetation includes cacti, yucca, sotol, lechuguilla, and ocotillo, with sagebrush and creosote bush on valley flats.

The modern distribution of *Lysinoe ghiesbreghtii* is largely within the zone of seasonal temperate forest of southern Mexico and Central America, with some extension into wet optimum forest types. The localities for which definite information is available (see Appendix) are in Pine-Oak Forest, Pine Forest (a facies of Pine-Oak Forest), Pine-Oak-*Liquidambar* Forest, and Montane Rain Forest, of BREEDLOVE's (1981) classification of vegetational formations of Chiapas. The locality "Mosquito Coast, north of Cape Gracias-à-Dios" (Honduras) by MARTENS (1890–1901) is definitely in error; his record from Hacienda Buenavista, Guatemala, at elevation 4000–5000 ft (1219–1524 m), is lower in altitude than any material I have personally examined, although the appropriate forest types extend this low (BREEDLOVE, 1981).

The Pine-Oak Forest is an open forest association composed of relatively few species of trees. Stands of pure pine or oak occur in specialized edaphic situations. The trees are commonly 15–40 m tall and variably spaced. Epiphytes are sparse to common but heavy only in canyon situations. The understory is usually herbaceous with a few shrubs (BREEDLOVE, 1981).

The Pine-Oak-*Liquidambar* Forest is a diverse plant association with many species of deciduous and semi-deciduous trees, an abundance of epiphytes, and a variable understory ranging from a dense association with many species of shrubs, subshrubs, and vines, to a tall grassy expanse with scattered shrubs. This formation is less open than Pine-Oak Forest; the trees, which may be quite broad-crowned, usually are close enough for their crowns to form a continuous canopy. This is a temperate forest quite similar to the diverse hardwood forests of the southeastern

United States, and depauperate elements of this association occur at scattered locations in the Sierra Madre of central and northern Mexico (BREEDLOVE, 1981; MIRANDA & SHARP, 1950).

Pine-Oak Forest ranges in altitude from 1300 to 2500 m with occasional patches as low as 1000 m. It exists where there is a dry season of from three to six months. Where the dry season is three months or less, it is replaced by Pine-Oak-*Liquidambar* Forest. Where a dry season is absent or at most only a few weeks in length, Pine-Oak-*Liquidambar* Forest is replaced by Montane Rain Forest or, above 2500 m elevation, by Evergreen Cloud Forest (data from BREEDLOVE, 1981, fig. 5, and personal communication). Rainfall is an important determinant of local vegetational type, as seen in the difference between east and west escarpments of the Chiapas Plateau: Pine-Oak-*Liquidambar* Forest and Montane Rain Forest cover the eastern escarpment; Pine-Oak Forest and Tropical Deciduous Forest occur on the drier west side (BREEDLOVE, 1981).

At San Cristobal de las Casas (16°44'N, 92°38'W; elev. 2755 m), typical of stations within the Pine-Oak Forest, mean annual temperature is 14.8°C and there is a mean annual range of temperature of 3.5°C. The normal mean temperature for the coldest month (December) is 12.5°C; that for the warmest months (June and July) is 15.9°C. Annual rainfall is 123 cm, 6 cm of which (less than five per cent of the annual total) falls in the period from November through February (GARCÍA, 1973). Such a climate is classified as temperate and moist, with a long cool summer (GARCÍA, 1973). Using the data of mean annual temperature and mean annual range of temperature, the nomography method (AXELROD & BAILEY, 1969) gives estimates of 197 days per year warmer than 14°C, a virtual absence of freezing temperatures, and an equability rating of 82. (Equability, as defined by Axelrod & Bailey, here means freedom from extremes of both heat and cold. A rating of 82 indicates an exceptionally equable climate.)

The rock enclosing the samples of *Lysinoe breedlovei* from the Colmena Tuff is a pinkish-brown tuffaceous siltstone, probably rhyolitic in composition, with interstitial iron oxide staining. It was undoubtedly water-laid (J. F. DeMouthe, personal communication) and suggests a humid rather than an arid climate. During deposition of the lower sedimentary facies of the Colmena Tuff, the area was apparently a broad valley occupied by meandering streams with active volcanoes not far distant (WILSON, 1978).

By analogy with *Lysinoe ghiesbreghtii*, *L. breedlovei* indicates a highly equable, moist, temperate climate, either with or without a winter dry season. The landscape was forested with vegetation like the present-day seasonal temperate forests of Chiapas (Pine-Oak or Pine-Oak-*Liquidambar*) or, possibly, Montane Rain Forest. Perhaps an analysis of the mammals of the Candelaria local fauna, when all groups have been worked up, will indicate whether a dense formation—Pine-Oak-*Liquidambar* or

Montane Rain Forest—or the relatively open Pine-Oak Forest is the more likely. There would have been a minimum of 123 cm of precipitation annually.

*Lysinoe ghiesbreghtii* lives at altitudes of about 1800–2700 m. The regional geology of Trans-Pecos Texas indicates that the rocks of the Vieja Group formed at lower elevations and have been raised to their present altitude (1000–2000 m) since Eocene time. The strata containing the Barrilla flora in the neighboring Davis Mountains, probably contemporaneous with the Chambers Tuff, were most likely deposited at or below 300 m altitude (AXELROD & BAILEY, 1976). Fossil floras of the Rio Grande depression, New Mexico, have undergone 1200 m of post-Eocene uplift (AXELROD & BAILEY, 1976). The specimens of *L. breedlovei* from Nuevo León were deposited in a brackish marine environment and probably transported no great distance from the interior; here also a lower elevation is indicated. Although the precipitation and thermal parameters are inferred to have been similar to those of the modern temperate Mexican forests, the topographic setting was probably much lower and in more direct communication with the coastline.

The information available on the modern habitats and environments of the other genera is much less complete or, in the case of *Xerarionta*, spans a broader range of conditions.

Locality records of *Polymita picta* (morphologically the closest species to *P. texana*) in the CAS collection indicate that the species occurs on forested terraces inland from Maisí, Oriente Province, over an altitude range of at least 180–460 m and elsewhere along the northeastern coast at least as far west as Punta Guárico. The vegetation is seasonal tropical forest with a high diversity of tree species, including *Cedrela mexicana*, *Ficus aurea*, *Ocotea leucoxydon*, *Pithecellobium saman*, *Roystonea regia*, *Spondias mombin*, and *Zanthoxylum* species (SEIFRIZ, 1943). Normal annual rainfall in the range of *P. picta* is 114–152 cm. (At Punta Maisí proper, one of the driest parts of Cuba and probably drier than the terraces inland, the annual precipitation is 78 cm [PORTIG, 1976].) For Oriente Province as a whole the driest season is December through April; in each of the months January through March there is less than 6 cm of precipitation (SEIFRIZ, 1943, fig. 6). At Punta Maisí the mean annual temperature is 26.3°C and there is a mean annual range of temperature of 4.5°C (PORTIG, 1976). The equability rating determined by nomography is 43. This is a true tropical climate with the normal mean temperature of the coldest month above 18°C. The vegetational and thermal relations are inconsistent with those based on *L. ghiesbreghtii*, although the general indications of rainfall and a winter dry season are compatible.

There is inadequate information on the total range of *Pleurodonte (Dentellaria) anomala*, the modern species similar to the *Dentellaria* of the Porvenir local fauna, but it does occur near Mandeville, Jamaica (PILSBRY & BROWN, 1910), on the bauxitic Manchester Plateau. Here the original forest has been much modified by agriculture

and grazing, but the tree species are elements of the Wet Limestone Forest, a seasonal formation (ASPREY & ROBBINS, 1953). Rainfall is between 150 and 200 cm annually with "few months" with less than 10 cm. The climate is tropical.

*Pleurodonte* (*Pleurodonte*) occurs in the Lesser Antilles; *P. (P.) isabella*, one of the species similar to *P. (P.) wilsoni*, lives on Barbados. At Bridgetown, Barbados, the annual rainfall is 130 cm; at Dunscombe it is 218 cm (PORTIG, 1976). March is the driest month, August the wettest. At Bridgetown the mean annual temperature is 26.3°C and there is a mean annual range of temperature of 2.0°C. The equability rating is 44. The climate is, therefore, similar to that in the range of *Polymita picta*.

*Xerarionta* now occurs on the southern California Channel Islands and the adjacent mainland, and along the western part of Baja California between latitudes 24–31°N. The Baja California occurrences are all within the arid, subtropical to tropical Sonoran Desert. Avalon, Santa Catalina Island (in the range of *X. kelletii*), has a mean annual temperature of 14.5°C and a mean annual range of temperature of 7.2°C, an equability rating of 72, and annual precipitation of about 33 cm (ELFORD, 1970). Representative stations within the Sonoran Desert range of the genus include El Rosario (mean annual temperature 17°C; mean annual range of temperature 10°C), Bahía Magdalena (21.5°C; 8.5°C), and Vizcaíno (19°C; 8.5°C) (AXELROD, 1979, fig. 3). Equability ratings range from 54 to 64. The nomogram indicates more than 212 days warmer than 15°C at El Rosario, more than 281 days warmer than 17°C at Bahía Magdalena. These are among the mildest and least thermally variable stations in the Sonoran Desert.

The development of the Sonoran Desert as an arid environment of regional extent was an event of latest Tertiary and Quaternary time (AXELROD, 1979). Older environments of Tropic Savanna, Dry Tropic Forest, Short-tree Forest, and drier formations contributed the ancestors of the plant taxa that now characterize the desert. While it is not justifiable to conclude that *Xerarionta waltmilleri* lived under arid conditions, on the analogy of plant history it may have been an inhabitant of relatively xeric sites in a seasonally dry tropical or subtropical forest.

From the composition of the Rancho Gaitan local fauna of northeastern Chihuahua (early Chadronian, correlated with the Little Egypt local fauna), FERRUSQUÍA (1969) inferred a woodland community, possibly with marshy habitats, and (from the presence of "thousands" of large fresh-water gastropods) the existence of a neighboring body of permanent water. Thermal parameters were not specified.

AXELROD & BAILEY (1976) interpreted a small fossil flora from the Huelster Formation in the Barrilla Mountains to represent the upper part of a dry mixed subtropical flora, analogous to modern vegetation in southern Tamaulipas and southward along the east front of the Sierra Madre Oriental. The Huelster Formation is correlated

with the Chambers Tuff (both are overlain by volcanics yielding radioisotopic ages in the 36–37 Ma range: WILSON, 1978, table 15), so climatic inferences from the Barrilla flora may also be applicable to the neighboring Chambers Tuff.

Increasing amounts of caliche cement in the sediments of the Chambers Tuff indicate that increasingly drier conditions prevailed at the time of that unit's deposition (HARRIS, 1967, M.A. thesis, Univ. Texas Austin; *vide* FERRUSQUÍA, 1969). WILSON (1978:32) also concluded that the paleoenvironment of the Chambers Tuff was "more open than that of the Colmena, more removed from direct volcanic activity and probably dryer."

In the Sierra Vieja area, *Lysinoe breedlovei* makes its last appearance in the lower part of the Chambers Tuff; its last appearance in the Agua Fria–Buck Hill area is probably not much later in time. Its local disappearance may be correlated with increasing aridity and/or decreasing equability of climate. During this interval its range may have begun to retreat southward, and possibly altitudinally upward—where the likelihood of preservation in lowland basins would be less. *Xerarionta waltmilleri* makes its first appearance in the upper part of the Chambers Tuff. The presence of this genus is consistent with drier and at least somewhat less equable conditions.

The climatic transition cannot have been too radical, however, because *Pleurodonte wilsoni* remained present throughout the interval represented by the Porvenir to Ash Spring local faunas.

The sympatry in the Vieja Group of land mollusk genera now widely separated is striking. *Polymita*, now restricted to the eastern province of Cuba, was sympatric with *Lysinoe* in western Texas during late Uintan time. Two now allopatric subgenera of *Pleurodonte* coexisted in early Chadronian time; *Lysinoe* has not yet been found at the same localities with them but comes from related sites yielding the Porvenir local fauna. *Pleurodonte* and *Xerarionta* were sympatrically associated with the Little Egypt local fauna. The history of these genera since early Tertiary time has involved both southward limitation of range and assortment into different geographic areas. How much of this change represents sorting out along environmental gradients and how much is attributable to historical accident remains a subject for investigation. At present, and presumably to a greater or lesser extent throughout the Tertiary, a southward geographic shift from North America takes a taxon into an area of smaller and more disjunct land masses, where isolation and the probability of chance extinctions are higher.

In the late Eocene paleogeographic reconstruction of the Caribbean region by SYKES *et al.* (1982, fig. 11), the various land masses now inhabited by the genera of the Vieja Group assemblage were more closely juxtaposed. The Caribbean Plate, including Central America south of the Motagua Fault, Jamaica, and the region of the Lesser Antilles, was some 1400 km farther west than at present. Jamaica is pictured as adjacent to southern Mexico, the

Lesser Antilles directly south of eastern Cuba. Somewhat earlier, 48 million years ago, Cuba was part of the East Pacific-Caribbean Plate and adjacent to the Yucatan Peninsula (SYKES *et al.*, 1982, fig. 9, top). The separation of Baja California from mainland Mexico by the rifting open of the Gulf of California is a relatively young event, perhaps beginning only four million years ago, although a proto-Gulf of California, resulting from extension behind a trench-arc system, may have existed as early as the Miocene (KARIG & JENSKY, 1972).

These paleogeographic reconstructions do not, however, eliminate the need to consider over-water dispersal in the biogeography of Caribbean land snail genera. They merely change the map on which hypothetical routes of dispersal must be plotted. For instance, depending on the (conjectural) emergence of the Nicaragua Rise, *Lysinoe* may have reached the portion of Central America on the Caribbean Plate either over water or by land in Paleogene time; or it may have made a shorter trip by land when Central America and Mexico became juxtaposed in the Miocene, between 20 and 7 Ma (SYKES *et al.*, 1982, fig. 9, center and bottom).

Sympatry of taxa now widely separated is proving to be a common phenomenon in Tertiary faunas of western North America (ROTH, in press). The same has been found true for plants (AXELROD & BAILEY, 1969:178-179):

"No Tertiary flora is duplicated exactly in any one area by modern vegetation. In part the problem [in analyzing paleoclimates] is one of species extinction, but also troublesome is the fact that living plants most similar to those of a fossil flora regularly contribute to forests that live in widely separated regions, and under different climates. For example, Miocene floras from central California to Washington are composed of plants whose nearest relatives are found in the conifer forests of the western United States, in the mixed deciduous hardwood forests of the eastern United States and in the related forests of China and Japan."

The property of equability, permitting year-long growth, and the absence of frost permit tropical plants to live together with many species found in temperate regions, as occurs in the Sierra Madre Oriental of Mexico (MIRANDA & SHARP, 1950; AXELROD & BAILEY, 1969) and in the zone of seasonal temperate forest in Chiapas. Climates of high equability were widespread in North America during the Eocene (AXELROD & BAILEY, 1969). The vegetation of the Mexican areas mentioned (including the Chiapas Plateau) includes a considerable number of species, among them the forest-dominant oaks and pines, that seem to have had a northern origin and relationships (MIRANDA & SHARP, 1950). The similarity of the Pine-Oak-*Liquidambar* Forest to the hardwood forests of the southeastern United States has already been mentioned: many plant species in eastern Mexico have very similar or identical counterparts in the eastern U.S. Miranda & Sharp regarded 16% of 200 species that occur frequently in the major temperate communities of eastern Mexico as be-

longing to this category. GRAHAM (1973) listed 21 identical species and 12 species-pairs among the arborescent (tree and shrub) genera common to the eastern U.S. and eastern Mexico. The distributions of these species and species-pairs are now disjunct (compare MIRANDA & SHARP, 1950, fig. 12), but the evidence points to a former continuity around the northwest Gulf of Mexico and for unknown distances further north and west. The finding of *Lysinoe*, a snail associated with the temperate Mexican forests, in the Eocene of western Texas, supports this scenario. However, the presence of other snail genera now inhabiting more tropical forests suggests that the forest elements may already have been somewhat mixed.

In summary, the land mollusk sequence is consistent with a transition, over late Uintan-early Chadronian time, from a highly equable, moist and temperate climate to one more arid and less equable. The beginning of the southward retreat of the ranges of several modern genera may be in evidence. Genera now allopatric were formerly sympatric. On the model of plant communities, climatic equability is probably an important factor regulating northern range limits, and perhaps generic diversity as well.

#### ACKNOWLEDGMENTS

For the opportunity to study Vieja Group land snails, I thank John Andrew Wilson and Dwight W. Taylor. Drs. Wilson, Jason A. Lillegraven, Walter B. Miller, Alan Solem, Eugene V. Coan, and David R. Lindberg have read drafts of the manuscript and made helpful suggestions. I am grateful to Dennis E. Breedlove for information on the modern habitat of *Lysinoe* and its climatic implications, and deeply indebted to him, Luis F. Baptista, Kenneth E. Lucas, and others who collected mollusks in Chiapas for the California Academy of Sciences (under permit from the Secretaria de Agricultura y Ganaderia). Fred G. Thompson supplied information on *Lysinoe* in the Florida State Museum. Melissa Winans (TMM) and David R. Lindberg (UCMP) kindly made available specimens from the collections under their care. Jean F. DeMouthe contributed a lithologic analysis. Thomas R. Waller, Frederick J. Collier, and Jann Thompson advised on specimens in the USNM. Frank Almeda and Peter U. Rodda (CAS) facilitated the investigation in various ways. SEM photographs were taken in the SEM facility of the Department of Entomology, CAS, with competent aid from Mary Ann Tenorio and Eduardo Almeida. Photographs 1-14 are the work of Jeanne M. Lynch. Breedlove's field work in Chiapas was supported by National Science Foundation grants GB-29483x, DEB-7912213, and DEB-7923274. A donation by Mrs. Rozaline Johnson supporting illustration of the paper is gratefully acknowledged.

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## APPENDIX:

Locality Records for *Lysinoe gheisbreghtii*

*Mexico*: Chiapas: Municipio Teopisca, 10 km N of Teopisca, elev. 7000 ft (2134 m), D. E. Breedlove coll., 21 Oct 1981 (CAS 029679). In hills on E side of San Cristóbal de las Casas, elev. 7400 ft (2255 m), D. E. Breedlove coll., 22 Aug 1981 (CAS 029680). Aguacutenango, elev. 5900 ft (1798 m), pine-oak forest, D. E. Breedlove coll., 12 Jun 1966 (CAS 037059). Rancho Nuevo, 8.6 mi SW of San Cristóbal de las Casas, elev. 7800 ft (2377 m), pine forest, L. Baptista coll., 19 Aug 1966 (CAS 037066). Near San Cristóbal de las Casas, elev. 7000 ft (2134 m), E. Hunn coll., 15 Nov 1971 (CAS 037065). At km 1156 on Highway 190 between Chiapa del Corzo and San Cristóbal de las Casas, elev. 7750 ft (2362 m), pine-oak forest, L. Baptista coll., 18 Aug 1966 (CAS 037062). Seventeen kilometers SE of San Cristóbal de las Casas, pine-oak forest, elev. 2195 m, D. E. Breedlove & K. E. Lucas coll., 15 Jan 1973 (CAS 037061). Along small stream on Cerro Tres Picos, elev. 7000 ft (2134 m), D. E. Breedlove coll., 28 Mar 1973 (CAS 037060). Two to four kilometers SW of Highway 190 along road to San Lucas Zapotal, elev. 7500 ft (2286 m), D. E. Breedlove coll., 8 Sep 1974 (CAS 037064). Ten and one half miles SW of San Cristóbal de las Casas, K. E. Lucas coll., 2 Sep 1972 (CAS unnumbered). SE side of Cerro Tres Picos, montane rain forest, elev. 6000 ft (1828 m), D. E. Breedlove coll., 28 May 1972 (CAS unnumbered). E side of Cerro Bola just E of Tres Picos, elev. 6000 ft (1828 m), D. E. Breedlove coll., 4 May 1972 (CAS unnumbered). Near San Cristóbal, E. Hunn coll., 1971 (CAS unnumbered). Laguna Chamula, microwave tower between Comitán and Amatenango, elev. 8300 ft (2530 m), 20 Aug 1972 (CAS unnumbered). Zinacantán, elev. 2000 m (BEQUAERT, 1957). Environs of Chiapa (FISCHER & CROSSE, 1870-1902). Rancho Nuevo, 8 mi from Las Casas (BEQUAERT, 1957). Mountain above the Sumidero near Las Casas (BEQUAERT, 1957).

*Guatemala*: Mountains of Alta Vera Paz (FISCHER & CROSSE, 1870-1902). Cobán (FISCHER & CROSSE, 1870-1902; MARTENS, 1890-1901). Purula, towards the head of the Polochic valley (MARTENS, 1890-1901). Cerro Zunil, on the Pacific slope, near

Quetzaltenango (*ibid.*). Hacienda Buenavista in Upper Cholutz, elev. 4000-5000 ft (1219-1524 m), in forests (*ibid.*). Depto. Solola, Toliman, in the hills above San Lucas, near the lake of Atitlán, temperate zone (FISCHER & CROSSE, 1870-1902;

MARTENS, 1890-1901). Duena (FISCHER & CROSSE, 1870-1902).

*Honduras*: Cordillera of San Marcos, elev. about 2660 m (FISCHER & CROSSE, 1870-1902; MARTENS, 1890-1901).

*El Salvador*: Volcan de Santa Ana (BEQUAERT, 1957).